Chapter 10

Simulating Crop Phenological Responses to Water Deficits

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Abstract

Accurate phenology algorithms are fundamental for accurate simulation of crop growth. Phenology frequently changes as water becomes limiting, but such responses are poorly understood and difficult to quantify. Thus, these phenological responses are often ignored when modeling phenology. This chapter reviews the effects of water deficits on crop phenology and examines approaches used to simulate phenological responses to changes in water deficits. The dominant factors determining development rate are described, with particular attention given to the concept of thermal time and the correlation between thermal time and crop development rate for different phases of plant development. A survey of the literature to identify diverse phenological responses to water stress across species and genotypes is presented. Possible reasons for differences are discussed, and four mechanisms explaining phenological responses to water deficits are postulated. Different approaches for simulating phenological responses to changes in water deficits are described. Suggestions for improving the modeling of phenological development under water deficits are provided.

Response of crops to limited water: Understanding and modeling water stress effects on plant growth processes.
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The relationship between air temperature and the timing of developmental events has been long recognized (Reamur, 1735). This basic relationship provided the seminal idea for initial simulations of crop development. As our understanding of crop development and management increased, it became clear that knowledge of the timing of phenological events in crops is essential for effective management. Similarly, the importance of accurately simulating the timing and sequence of developmental events from seed germination to physiological maturity is well known. If developmental responses to the environment (directly or via management practices) are poorly quantified, then predictions of simulated growth, nutrient and water use, and final yield will likely have substantial errors. Such errors arise because growth processes will be simulated for different environmental conditions than occurred in the field and because the sequence of developmental events affects the activity of sources and sinks, which in turn affects the processes of resource capture, partitioning, and remobilization.

Reflecting the importance of development, simulation of phenology has received considerable attention (Ritchie and NeSmith, 1991; Jamieson et al., 2007), although arguably less than needed relative to simulations of photosynthesis, water balance, and nutrient uptake algorithms. Most simulation models consider the influence of water deficits on plant processes (e.g., photosynthesis, nutrient uptake, and growth), yet few models deal explicitly with the effects of water deficits on phenology. This chapter reviews the effects of water deficits on phenology and then examines approaches used to simulate phenological responses to water deficits. Strategies for improving simulation of phenological responses to water deficits are suggested at the end of the chapter.

Phenological Responses to Water Deficits

Crop development has been extensively reviewed elsewhere (e.g., Hay and Porter, 2006; Hodges, 1991; Ritchie and NeSmith, 1991), so emphasis here is on modeling phenological responses to water deficits. Phenology can be viewed as the result of integrating rates of development over time up to specific endpoints that correspond to developmental events or stages such as onset of flowering. Therefore, the life cycle of an annual seed crop is viewed as progressions through phases of

development, demarcated by familiar stages such as seedling emergence, flower initiation, onset of flowering, onset of seed growth, and physiological maturity (Table 10–1). The rate of development is influenced by air temperature, and may be influ-

Table 10–1. Qualitative influence of water deficits on developmental stage progression.

Crop	Flower initiation	Flowering	Duration of seed filling	Physiological maturity	Sources
Barley (*Hordeum vulgare* L.)	0?	+†	+	+	McMaster and Wilhelm (2003, 2005)
Chickpea (*Cicer arietinum* L.)		+	+	+	Johansen et al. (1994)
Cotton (*Gossypium hirsutum* L.)		0/+	+	-/0/+	El-Zik et al. (1977), Grimes et al. (1978), Guinn et al. (1981)
Dry bean (*Phaseolus vulgaris* L.)	0	0/+	+	+	Robins and Domingo (1956), White and Izquierdo (1991)
Maize (*Zea mays* L.)		–‡	+	+	Campos et al. (2004), Farre and Faci (2006), Jama and Ottman (1993), McMaster et al. (2005), NeSmith and Ritchie (1992a,b,c), Rosales-Serna et al. (2004)
Peanut (*Arachis hypogaea* L.)		–	+	+	Ketring and Wheless (1989)
Sorghum [*Sorghum bicolor* (L.) Moench]		–	+	±?	Donatelli et al. (1992), Farre and Faci (2006), Gardner et al. (1981), Rosenow et al. (1983)
Soybean [*Glycine max* (L.) Merr.]			+	+	Constable and Hearn (1978), Sionit and Kramer (1977), Wolf (2002)
Sunflower (*Helianthus annuus* L.)	0		+	+	Anderson et al. (1978), Marc and Palmer (1976)
Wheat (*Triticum aestivum* L.)	0?	+	+	+	McMaster and Wilhelm (2003, 2005).

† + symbol indicates earlier occurrence of the event under water deficits, – symbol indicates later occurrence of the event under water deficits, 0 symbol indicates no response under water deficits. Question marks indicate conflicting or uncertain responses. Blank cells indicate no literature reports were found for the developmental event. Developmental stages are defined as: (i) flower initiation is the appearance of the inflorescence/flower primordium; (ii) flowering is the appearance of flowers (and often the start of pollen shed, or anthesis); (iii) duration of seed filling is from pollination (assumed to coincide with flowering and anthesis) to physiological maturity; and (iv) physiological maturity is when maximum seed dry weight occurs.

‡ Both anthesis and silking are delayed, but silking is delayed more resulting in a longer anthesis–silking interval.

enced by photoperiod, and nutrient and water availability. The direction of these influences on specific developmental events varies (e.g., McMaster, 1997; Fig. 10–1).

If the effects of air temperature are accounted for, phenology is often observed to be remarkably stable over a wide range of growing conditions, despite plants of dramatically different size and appearance within a given cultivar. The underlying explanation for the stability is that plants mark the passing of time via thermally driven internal biological clocks (Thain et al., 2002; Millar, 2004; Hotta et al., 2007). One consequence of the internal clocking is that phenology is predicted surprisingly well with simple models, most based on a relationship with air temperature as an estimate of the movement of the internal clock.

As mentioned in the introduction, Reamur (1735) was the first to predict phenology by relating developmental events to air temperature. He proposed the concept of heat units, which has since evolved into the more general notion of thermal time. Thermal time in its basic form has two components: (i) the integral, or accumulation, of temperature over some time interval; and (ii) use of this integral in a temperature response function to calculate thermal time (although sometimes the second component is not used). Thermal time typically is expressed in units of degree–days (°C d). Many approaches have been developed for calculating thermal time. The time interval normally may range from hourly to daily time steps. The temperature response function can be a simple linear function with either an upper and/or lower threshold limitation or no

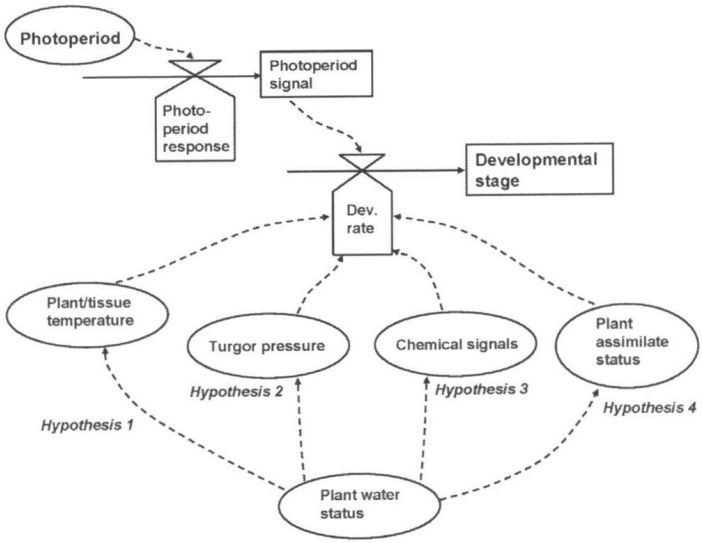

Fig. 10–1. Simplified Forrester diagram of possible mechanisms for water deficits to influence crop phenology.

limitations (McMaster and Wilhelm, 1997), or more refined such as a segmented linear function or a curvilinear response function (Jamieson et al., 2007; Streck et al., 2003; Yan and Hunt, 1999). Three cardinal temperatures are required in these more refined temperature response functions to determine the effectiveness of the integrated temperature for each time step on development rate. These cardinal temperatures are a base temperature, below which no development occurs; a maximum temperature, above which no development occurs; and an optimum temperature, where development rate is maximum. The intervals between these cardinal temperatures can be linear or nonlinear.

Beginning in the 1970s, a refinement to using thermal time was proposed. This refinement was to use the phyllochron, or leaf appearance rate, to represent the internal biological clock for measuring the time between developmental events (e.g., Rickman and Klepper, 1995; McMaster, 2005; Wilhelm and McMaster, 1995). In part, this approach was also driven by the realization that thermal time to maturity for wheat (*Triticum aestivum* L.) was negatively correlated with planting date (e.g., Nuttonson, 1948), and a relationship could be developed between change in photoperiod at planting date and the phyllochron (Baker et al., 1980). This approach is used in such models as SHOOTGRO (McMaster et al., 1992a, 1992b; Wilhelm et al., 1993), and MODWht (Rickman et al., 1996), where the number of leaves that appear between developmental events is used rather than a constant thermal time estimate to predict development stages from emergence to anthesis. The Sirius model (Jamieson et al., 1998a, 1998b) uses leaf appearance and total number of leaves produced to predict developmental stages from emergence to anthesis. All models have shown some success in this approach, although Xue et al. (2004) found that a nonlinear approach to simulating winter wheat leaf appearance was superior to two other phyllochron models. Streck et al. (2003) improved this nonlinear approach by incorporating a chronology function into the function.

Photoperiod also can modify rates of development, as first demonstrated by Garner and Allard in the 1920s. The photoperiod response of many crops has been studied and quantified for use in simulation models (e.g., Streck et al., 2003; Ritchie and NeSmith, 1991). Cultivars often differ in photoperiod sensitivity and increasingly, genetic and molecular studies are revealing underlying mechanisms. Examples of this include positional cloning of the *Ppd-H1* locus for barley (*Hordeum vulgare* L.) photoperiod response (Turner et al., 2005); the *VRN1*, *VRN2*, and *VRN3* vernalization loci in wheat (Yan et al., 2003, 2004, 2006); and the *Ma3* maturity locus related to phytochrome B synthesis in sorghum [*Sorghum bicolor* (L.) Moench; Childs et al., 1997]. Understanding gene networks involved in con-

trolling flowering is rapidly advancing from *Arabidopsis thaliana* (L.) Heynh. to crop plants such as barley (e.g., Laurie et al., 2004).

Environmental factors such as water and nutrient availability also influence development. Seeds usually require a threshold water content before germination begins, after which temperature (and the continued availability of water) influences the rate of development. In wheat and barley, early developmental stages such as jointing and flag leaf appearance showed little response to soil water availability. Later developmental stages such as anthesis and physiological maturity occurred as much as 13 and 15 d (or over 360 growing degree-days) earlier, respectively, under severe drought conditions (i.e., less than half of long-term mean growing season precipitation; McMaster and Wilhelm, 2003). In maize (*Zea mays* L.), anthesis and silking occurred slightly later under water-stressed conditions and the anthesis–silking interval increased (Campos et al., 2004). Abrecht and Carberry (1993) reported that when severe water stress was imposed for 19 d following emergence, maize silk and tassel initiation were delayed, primarily by slowing the rate of leaf appearance, but subsequent developmental stages were reached earlier, somewhat contradicting other observations such as those reported by Campos et al. (2004).

The various responses to water deficits demonstrate the need for rigorous assessment of how changing water deficits affect phenological responses on a species basis and for all developmental stages. Unfortunately, few summaries exist that synthesize the entire developmental sequence of shoot apices and correlate this with other developmental events under any environmental conditions. McMaster et al. (2005) published developmental sequences and phenological responses to water deficits between irrigated and severe (but not lethal) drought for wheat, barley, and maize. An example of these sequences is shown in Fig. 10–2 for sorghum, and phenological responses of sorghum to water stress are presented in Fig. 10–3. Similar developmental sequences have been developed (unpublished data, McMaster, 2008) for sunflower (*Helianthus annuus* L.), proso millet (*Panicum milaceum* L.), and hay millet [*Setaria italica* (L.) P. Beauv.], and are used in a computer program for simulating phenology in multicrop production systems (http://arsagsoftware.ars.usda.gov).

While such summaries provide a foundation, better quantification and verification of phenological responses to changing water deficits in these crops (and for descriptions of genotypic variation within a species) are needed. Furthermore, the approach should be expanded to other crops where simulation models are lacking. To partially address this need, a brief review of the phenological responses to water deficits for different crops is given in Table 10–1, based on the literature and unpublished studies. Compilation of this table proved difficult for several

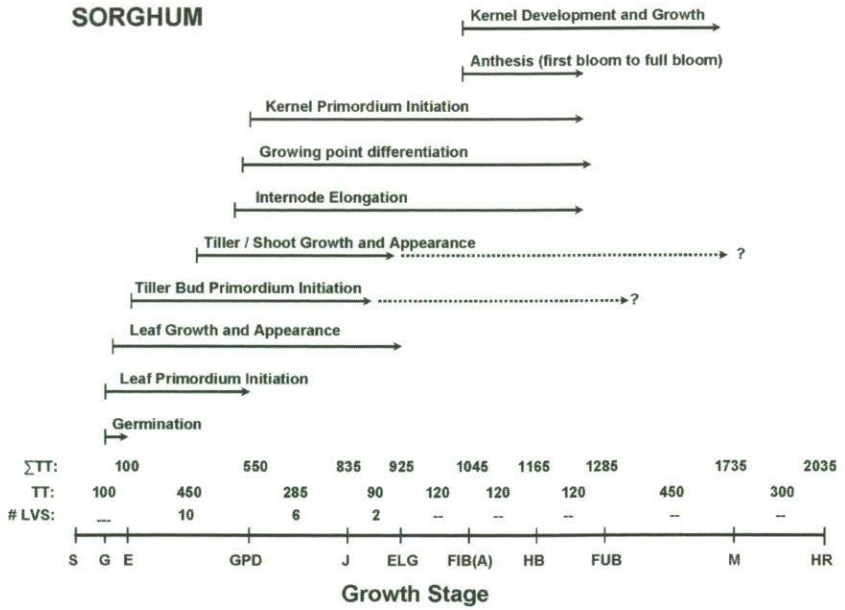

Fig. 10–2. Developmental sequence for "generic" temperate sorghum. Work is based on unpublished data and literature compiled by McMaster (2008), and modeled after the developmental sequences of McMaster et al. (2005). Thermal time (TT) is calculated by $(T_{max} + T_{min})/2 - T_{base}$ and $0°C \leq TT \leq 30°C$, where T_{max} is the daily maximum temperature, T_{min} is the daily minimum temperature, and T_{base} is the base temperature (10°C). The equivalent number of leaves (# LVS) is noted below the thermal time. See Fig. 10–3 for developmental event abbreviations.

SORGHUM

Water nonlimiting

	S	E	GPD	J	ELG	FIB (A)	HB	FUB	M	HR
TT:	100	450	285	90	120	120	120	450	300	
# LVS:	---	10	6	2	---	---	---	---	---	

Water limiting

	S	E	GPD	J	ELG	FIB (A)	HB	FUB	M	HR
TT:	100+?	450	285	90	145	145	145	350	225	
# LVS:	---	10	6	2	---	---	---	---	---	

S = Sowing
E = Emergence
GPD = Growing Point Differentiation
J = Jointing
ELG = End of Leaf Growth
FIB = First Bloom (Anthesis Starts)
HB = Half Bloom
FUB = Full Bloom
M = Maturity
HR = Harvest Ready

Fig. 10–3. Phenological responses for minimal and maximal (nonlethal) water deficits of a "generic" temperate sorghum. Work is based on unpublished data and literature compiled by McMaster (2008), and modeled after the developmental sequences of McMaster et al. (2005). Thermal time (TT) is calculated as given in Fig. 10–2. The equivalent number of leaves (# LVS) is noted below the thermal time.

reasons. First, most field experiments lacked treatments with severe water deficits early in the life cycle. Second, even supposedly "well-watered" treatments (i.e., those considered as fully irrigated) often show evidence of water deficits (e.g., Gardner et al., 1981; McMaster and Wilhelm, 2003). Third, although many physiological studies have detailed measurements of plant water relations, most of these studies failed to report effects on phenology. Perhaps most importantly, these field studies rarely report plant water relations throughout the crop cycle, rather they present results for only a few points in time. These reasons limited our ability in Table 10–1 to characterize the degree of water stress of the plant that likely is critical in understanding the variable phenological responses. Therefore, our primary objective was to qualitatively determine phenological responses to extremes of water deficits (e.g., fully irrigated compared with some level of reduced available soil water) in Table 10–1, and then quantify the responses if possible.

Responses to water deficits would be expected to be a function of the timing, intensity, and history of the stress, and species and genotypes respond differently. For instance, Gardner et al. (1981) applied varying levels of irrigation at different developmental stages for two sorghum cultivars. In general, no differences in phenological responses were observed for any water deficit for the two different cultivars. However, development of one cultivar was delayed about 10 d under the most severe water deficits, and the delay may have been caused by delayed emergence. Rosenow et al. (1983) found that sorghum cultivars differing for the stay-green trait responded similarly when severe water deficits developed slowly over the entire growing season, but when severe water deficits developed quickly near flowering, cultivars lacking the stay-green trait matured sooner. Donatelli et al. (1992) showed the severity of water stress from floral initiation to flowering for six sorghum genotypes did not influence flowering time until water stress reached a threshold level resulting in delays of up to 20% relative thermal time in flowering for all genotypes of nonstressed plants. These studies illustrate that water deficits are part of the response, but it is unlikely the plant has a constant response to the same water deficit. At some stages, the same water deficit will have a greater effect (e.g., flowering and grain filling as noted below), and often there is a genotype by environment interaction. Some assessment of acclimatization to the water deficit is needed in addition to the degree of the water deficit to fully describe genotype sensitivity to water deficits.

Other than emergence, developmental stages up to about flowering of many crops seem relatively unaffected by water deficits (Table 10–1). Sunflower leaf number is minimally influenced by water deficits, and when water deficits have been shown to influence leaf appearance rates the stress was quite severe and leaf appearance rates decreased with increasing stress (e.g., Marc and Palmer, 1976).

The formation of flower primordia at the shoot apex marks the shift from a vegetative to reproductive phase. As with leaf number, generally little response of the timing of flower primordia formation to water deficits was found (Table 10–1). Furthermore, for many crops flower primordia formation begins at a fairly early leaf number (e.g., about 2-leaf stage for spring wheat and barley, McMaster et al., 2005; about 6-leaf stage for maize, McMaster et al., 2005; and about 8-leaf stage for sorghum, Rosenow et al., 1983). As mentioned earlier, the minimal phenological response noted for early developmental phases is partly because in many environments, severe water deficits seldom occur early in the life cycle. Also, it might be indicative of examining only a few cultivars to represent a crop, hence large differences were not found due to few genotypes sampled.

The effects of water deficits on developmental stages become more pronounced from the onset of flowering and thereafter (Table 10–1). Under severe water deficits, cereal crops such as wheat and barley have earlier anthesis, while maize and peanut (*Arachis hypogaea* L.) show a few days delay of anthesis. Dry beans (*Phaseolus vulgaris* L.) show a range of response in flowering to water deficits from little response (White and Izquierdo, 1991) to a delay in flowering under the highest level of water deficits (Robins and Domingo, 1956). Sorghum and many perennial rangeland and forage grasses can show a considerable delay in flowering under severe water stress (Donatelli et al., 1992).

Part of this variation in flowering response to water deficits may relate to whether the wild progenitors of a given crop followed strategies of escaping (avoiding) or enduring (tolerating) water deficits, a difference closely related to annual or perennial growth habit, respectively. Annuals must produce seeds, and therefore will reduce investment in nonseed plant parts and processes as much as possible. Perennial plants have the option of delaying reproduction when the environment is extremely stressful and instead, focusing resources on responses that promote plant survival. For perennials, the need to develop and support the perenniating tissues (crown, bulbs, buds, etc.) complicates the situation, especially those that produce relatively large quantities of seeds. Indeed, producing seeds in severely limiting environments may lower the probability of successful establishment of new seedlings.

All seed crops appear to shorten seed-filling duration under water deficits (Table 10–1). Whether a shortened seed-filling duration under water deficits will change the time of physiological maturity is partly dependent on the timing of flowering in response to water deficits. In crops such as wheat and barley with earlier flowering and shortened seed filling under water deficits, physiological maturity will be reached earlier. For crops such as maize that slightly delay flowering but have accelerated seed filling under water deficits, physiological maturity

date under water deficit conditions may vary slightly around nondeficit conditions (McMaster et al., 2005). The shortened duration of seed filling in crops such as sorghum often is insufficient to offset the large delay in flowering under water deficits, resulting in delayed physiological maturity.

Across species and genotypes, plants display numerous phenological responses to water deficits. Part of the explanation for the multiplicity of responses is associated with different strategies to survive drought (by avoidance or tolerance). A better understanding of these responses may be gained by examining the components of each developmental event. Although cell division and expansion are a part of every developmental event, events can be distinguished by their "growth" (cell expansion) or "development" (cell division) components. For instance, production of a leaf or spikelet primordium on the wheat shoot apex is primarily an event of cell division. Development of the leaf primordium into a leaf is a result of cell division of the intercalary meristem and subsequent cell expansion and differentiation producing the leaf blade and sheath (McMaster et al., 2003b). Stem (i.e., internode) elongation is primarily cell expansion of newly formed cells from cell division of the intercalary meristem near the node, with heading in grasses merely the sum of internode elongation. Similarly, seed development is characterized by early dominance of cell division for the embryo and endosperm (approximately the first third of seed development) followed by cell expansion (approximately the last two-thirds of seed development; McMaster, 1997; Herzog, 1986). The variable response of different developmental events to water deficits may have some relationship with the "relative dominance" of cell division or expansion in the developmental event. As Hsaio (1973) discussed, cell expansion is extremely sensitive to water deficits, more so than cell division (which is more a function of temperature). Therefore, the phenological responses of developmental events with a large cell expansion component to water deficits (e.g., leaf appearance, internode elongation, and seed growth) might be expected to be particularly responsive to water deficits. A final point to consider is that genotypes can vary greatly in their ability to avoid or tolerate water deficits, and that many studies may be of limited value if a small selection of germplasm is used to characterize the species response.

Mechanisms Explaining Responses to Water Deficits

Our understanding of the processes underlying the variable phenological responses to water deficits outlined in Table 10–1 is incomplete, and substantial research on the physiology and associated genetics remains to be done. Nonetheless a series of mechanisms can be postulated to explain the observed responses,

particularly for the timing of anthesis and physiological maturity (and therefore duration of seed filling). The hypotheses are not mutually exclusive, and it is doubtful that a single hypothesis fully explains all observed responses.

Hypothesis 1: Water deficits lead to reduced stomatal conductance and transpiration, thus increasing daytime canopy temperatures and altering development rates through a thermal response.

It is well established that water deficits cause stomatal closure and lead to higher canopy temperatures. Depending greatly on the environmental conditions (e.g., the level of water deficit, atmospheric humidity, solar radiation levels, and nutrition level), the increase in leaf temperature associated with reduced transpiration usually is only a few degrees under most circumstances (Hsaio, 1973), but under severe water deficits canopy temperatures can be much higher than air temperature. Ehrler et al. (1978) measured elevated temperatures of up to 9°C for wheat, and Gardner et al. (1981) observed temperature differences of over 6°C for sorghum. The ability to accurately (and inexpensively) measure canopy temperature is continually improving, and some crop simulation models (e.g., ECOSYS, Grant et al., 1995; Sirius, Jamieson et al., 1998a, 1998b) calculate crop energy balances, including dynamic estimations of canopy temperature.

Elevated canopy temperatures may influence development, but only when the differentiating tissue is located in the canopy. This is because normally air temperature above the canopy (and occasionally soil temperature at the depth of the shoot apex) is used in calculating thermal time, and the assumption is that air/soil temperature gives an adequate relationship with plant temperature (e.g., shoot apex and intercalary meristems, and cell expansion zones of leaves and internodes). Clearly these relationships between plant tissue temperature and air temperature are affected by changes in canopy temperature due to water deficits. Thermal time approaches incapable of describing changes in canopy temperatures (either above or below air temperatures) resulting from changes in transpiration will not reflect even gross effects on crop development. However, the role of temperature on plant developmental rates is complicated by the fact that phenological processes occur in many different locations within the plant and that all parts of the plant (i.e., canopy and roots) are experiencing different temperatures. These different temperatures of different tissues can offset each other. In addition, temperature responses where the phenological process is occurring can change, or be changed by, supply of assimilates, nutrients, water, and chemical signals (McMaster et al., 2003b).

In evaluating this hypothesis, the variable phenological responses to water deficits for different crops, genotypes, and environments would be explained by

the degree of canopy temperature increase relative to the optimal temperatures for development. Elevated canopy temperatures would accelerate development if temperatures were below the optimum or slow development if temperatures were above the optimum.

Minimal responses of leaf number and flower initiation would partially be explained by the location of the grass shoot apex being belowground (at least for the leaves formed up to flower primordia initiation) or in the lower part of the canopy. In these instances, the role of canopy temperature will be negligible, if in fact canopy temperature is even elevated under these conditions. Conceivably, soil temperatures near the surface (down to 5 cm), and therefore shoot apex temperatures during phases before jointing in small grains, may be warmer than air temperatures. Certainly, when the soil is moist, soil temperatures at shoot apex depths (2–4 cm below the surface) are subject to less diurnal fluctuation than air temperature. The reverse may be true when the soil is dry.

Data from a field experiment conducted in eastern Colorado can be used to test this hypothesis (McMaster and Wilhelm, 2003). For each of 2 yr, the three winter wheat cultivars showing the greatest difference between dryland and irrigated treatments for the intervals of flag leaf complete to anthesis and anthesis to maturity are shown in Table 10–2. Using the simplest thermal time approach where temperatures above the optimum do not slow development (and would invalidate this hypothesis), the increase in canopy temperature above the air temperature needed to explain the earlier occurrence of anthesis and physiological maturity observed in the dryland treatments are shown (Table 10–2). The

Table 10–2. Increase in daily canopy temperature required to explain thermal time differences between dryland and irrigated dates of anthesis and physiological maturity for wheat.†,‡

Cultivar	Flag leaf–anthesis	Cultivar	Anthesis–maturity
	+ °C		+ °C
1999–2000			
1. TAM 107	24	1. 2137	19
2. Arlin	18	2. Siouxland	12
3. Akron	10	3. Prowers 99	11
2000–2001			
1. Prowers 99	12	1. Norstar	34
2. Alliance	9	2. TAM 107	22
3. Akron	3	3. Arlin	19

† The temperatures noted in the table were added to the daily maximum air temperature in calculating the thermal time for the dryland treatments where for the interval from flag leaf growth completed to anthesis or anthesis to maturity so that the thermal time in the dryland treatment equaled the thermal time in the irrigated treatment. The three cultivars in descending order with the greatest response for a phase to water deficits are presented. (Twelve cultivars were observed, with Halt, Heyne, and Yumar never ranking in the top three responses to water deficits.) Data from McMaster and Wilhelm (2003) for the Fort Collins, CO, site.

‡ Thermal time = $[(T_{max} + T_{min})/2] - T_{base}$ (Thermal time ≥ 0) where T_{max} is the daily maximum temperature, T_{min} is the daily minimum temperature, and T_{base} is the base temperature.

necessary increase in canopy temperature in all instances except one was much above observed or reasonably expected canopy temperatures (e.g., 9°C or more). However, for cultivars showing smaller phenological responses to water deficits (not shown in Table 10–2), this hypothesis accounted for much of the observed response.

Hypothesis 2: Under water deficits, lower water potentials are reflected in loss of turgor pressure and hence, tissue expansion or cell division is reduced, slowing development.

The critical role of turgor pressure in cell expansion has been long established and "in many species cell expansion is one of the plant processes most sensitive to water stress, if not the most sensitive of all" (Hsaio, 1973). This scenario suggests a seemingly logical relation whereby water deficits reduce tissue expansion through reduced turgor pressure. However, many lines of evidence subsequently suggest that plants actively maintain turgor by varying the osmotic potential (e.g., Kramer and Boyer, 1995; Morgan, 1977; Westgate and Peterson, 1993). The role of water deficits on cell division is also known to occur, but generally is less responsive to deficits than expansion (Hsaio, 1973). Some caution is needed in this perspective as it is difficult to observe, document, and study cell division compared with expansion. Therefore, the lack of published reports on cell division response of crops to water deficits is not surprising. As will be discussed under Hypothesis 3, a consensus is emerging that plants use specific chemical stress signals to regulate responses to water deficits rather than working directly through the physics associated with tissue dehydration as manifested through changes in water potential or turgor pressure.

Hypothesis 3: In response to water deficits, chemical signaling triggers specific stress responses that can increase or slow development.

Root/shoot signaling involves multiple chemical messengers (Beveridge, 2000), but for water deficits, abscisic acid (ABA) produced in roots and transmitted via xylem to specific locations in the shoot is especially important (Zhang et al., 2006). Research on *Arabidopsis thaliana* (L.) Heynh. and rice (*Oryza sativa* L.) further suggest that ABA and ethylene interact to regulate rates of development (Yang et al., 2004; Barth et al., 2006). Indirect support for this hypothesis includes triggering of flowering in citrus trees by water deficits (e.g., Kozlowski and Pallardy, 2002). However, at this time it is unknown how to predict which developmental rates will be affected and the direction of the response, so this hypothesis is quite speculative and as stated is not very testable.

Hypothesis 4 (relates to grain filling duration primarily): Water deficits lead to reduced photosynthesis and assimilate supply (mainly via reduced leaf area through accelerated senescence, but also reduced light interception through leaf rolling or leaf movement, lower CO_2 uptake due to stomatal closure, etc.) causing the canopy to die and ending grain filling.

With reduced assimilate availability due to water deficits, the seed-filling period may be shortened simply because assimilate to fill seed is not available or drops below a minimal threshold (e.g., NeSmith and Ritchie, 1992a). The underlying assumption is that grain maturation occurs when seed fill ceases, regardless of whether the seed is completely filled. This hypothesis is distinct from Hypothesis 3 in that it does not assume a role of a stress signal transmitted from the root system. However, it would not preclude signaling from leaves or sites of assimilate storage (e.g., stems) to the growing seed.

While much research supports the correlation between assimilate supply and seed-filling duration, tests that separate this hypothesis from Hypotheses 1 and 3 are difficult to construct. Further, this hypothesis does not address phenological responses of other stages to water deficits, such as anthesis, and explain why the stages may be delayed. However, as with Hypothesis 1, it may partially explain observed shortening of the seed filling period under water deficits.

Simulating Phenological Responses to Water Deficits

Ecophysiological models vary greatly in their levels of physiological, morphological, and developmental detail, and in many cases do not directly simulate effects of water deficits on development. In many instances, not incorporating phenological responses to varying water deficits does not seem to be a great deficiency, both because of the overriding dominance of temperature in controlling phasic development and water deficits must reach a threshold of severity before changes in phenology are observed. However, the robustness and accuracy of models that do not simulate phenological responses to water deficits will be reduced because of instances where phenological responses to water stress have been observed. In this section, we examine how a number of models simulate phenological responses to water deficits as a basis for suggesting how the models might be improved in the next section.

In simple models, phenological development is specified directly as an input giving the calendar day for a developmental stage (e.g., Andales et al., 2005). This lessens or removes the need to simulate phenology, but requires observational data on the dates and lacks robustness for use under a wide range of environmental conditions and levels of water deficits. More developmental detail is provided

in models such as the EPIC-based plant growth models [e.g., EPIC, Williams et al., 1989; GPFARM, McMaster et al., 2003a; WEPP, Flanagan and Nearing, 1995; WEPS, Retta et al., 2001; SWAT, Arnold et al., 1995; and ALMANAC, Kiniry et al. (1992) models]. Thermal time in the EPIC-based models is calculated as:

$$\text{Thermal time} = [(T_{max} + T_{min})/2] - T_{base} \text{ (Thermal time} \geq 0) \quad [1]$$

where T_{max} is the daily maximum air temperature, T_{min} is the daily minimum air temperature, and T_{base} is the base temperature. Input parameters for the thermal time required between sowing and emergence, sowing and maturity, and percentage of life cycle (sowing to maturity, 0–1 scale) to several other stages such as start of grain filling and start of senescence for each crop must be supplied. This improvement marginally addresses limitations for the simple model approach in that generalized inputs are required compared with the date-specific inputs needed in the simple models. Models in this second category do not explicitly incorporate factors (e.g., photoperiod and vernalization) influencing phenology besides temperature, although in GPFARM different thermal time parameter estimates were provided for each crop based on whether irrigated or dryland conditions were being simulated. This addition improved model robustness (McMaster et al., 2003a). Parameterization with such an approach is complicated because phenological responses to limited soil water (i.e., severe but not lethal) have not been quantified for many crops, as noted above, and the parameters are species-specific and not genotype-specific so the genotype by environment interactions commonly observed are not addressed.

Other crop simulation models have incorporated considerable phenological detail and more mechanisms influencing phenology. To illustrate diverse approaches to simulating phenological responses to water deficits, our discussion will be limited to four models that demonstrate different conceptual approaches (CSM–CROPGRO, SHOOTGRO, Sirius, and PhenologyMMS).

CSM–CROPGRO

This model was originally developed from three grain legume models {soybean [*Glycine max* (L.) Merr.], peanut, and dry bean}, but is now available with templates for over 15 species (Jones et al., 2003; Hoogenboom et al., 2004). Development is simulated through integration of phase-specific rates based on hourly temperature data reconstructed from daily maximum and minimum air temperatures. Development rate varies with temperature, photoperiod, and water deficits, as well as cultivar. The effect of water deficit is based on empirically determined factors that change development rate as a function of an index of water stress. These factors vary considerably with phases and species (Table 10–3). For each

Table 10–3. Examples of phase-specific modifiers used to adjust developmental rates as a function of water deficit levels in the CSM–CROPGRO model (Jones et al., 2003; Hoogenboom et al., 2004). The modifers are unitless and have a multiplicative effect whereby negative values slow development and positive values accelerate it.

Developmental phase	Crop			
	Dry bean	Peanut	Soybean	Cotton
Planting to seedling emergence	–0.30	0.00	–0.20	–0.20
Emergence to first leaf	–0.30	0.00	–0.20	–0.20
Emergence to end of juvenile phase	–0.30	0.00	–0.40	–0.05
End of juvenile phase to floral induction	–0.40	0.00	–0.40	–0.05
Floral induction to first flower	–0.40	0.00	–0.40	–0.05
First flower to first peg (peanut only)	–0.40	0.00	–0.40	0.00
First flower to first pod or fruit	–0.40	0.00	–0.40	0.00
First flower to first seed beginning to grow	–0.40	0.00	–0.40	0.00
First seed to last seed	0.70	0.00	0.70	0.20
First seed to physiological maturity	0.70	0.00	0.70	0.20
Physiological maturity to harvest maturity	0.00	0.00	0.00	0.00
First flower to last mains stem leaf	–0.60	0.00	–0.60	–0.60
First flower to end of leaf growth	–0.90	0.00	–0.90	–0.90

developmental phase, the potential development rate is multiplied by a stress factor (FSW) calculated as:

$$FSW = 1 + [(1 - SWFAC) \times WSENP] \quad [2]$$

where SWFAC is a soil water stress parameter estimated based on the ratio between potential transpiration and readily extractable soil water, and WSENP is the phase-specific parameter, which can vary from –1 to 1 depending on crop species and developmental phase.

SHOOTGRO Model

The SHOOTGRO model (McMaster et al., 1992b; Zalud et al., 2003) simulates the phenology of each morphologically identified shoot (main stem and tillers) of several small grain species for the median plant of up to six age classes, or cohorts, based on time of seedling emergence. Soil water content determines the thermal time required for germination and seedling emergence rates. After germination, sequential developmental events are simulated using the number of leaves produced (e.g., phyllochron) between events up to anthesis, and thermal time after anthesis. SHOOTGRO explicitly includes the effect of water and N on phenology by adjusting the number of leaves or thermal time between developmental events

from emergence through maturity. A linear reduction in the number of leaves or thermal time is based on the resource availability index factor (which combines 0–1 water and N stress index factors) between upper and lower threshold values.

Sirius Model

The continuous development model of Jamieson et al. (1998a) is implemented in the Sirius wheat model (Jamieson et al., 1998b). Sirius does not follow the strictly sequential prediction of phasic development characteristic of many models. As with SHOOTGRO, Sirius assumes that the developmental "clock" from emergence to anthesis is best represented by the rate of appearance and final number of main stem leaves. The effects of vernalization and photoperiod are simulated through their effect on main stem final leaf number (Brooking, 1996; Brooking et al., 1995; Robertson et al., 1996). The rate of leaf appearance is driven by temperature but modified by ontogeny (Jamieson et al., 1995). Initially the controlling temperature is assumed to be that of the near soil surface, and then of the canopy. Sirius calculates near-surface soil temperature and canopy temperature based on the surface energy balance. Water deficit influences on phenology are not explicitly simulated, however canopy senescence is accelerated in water-limiting conditions resulting in shorter grain-filling duration due to loss of assimilate availability and thus maturity.

PhenologyMMS

The PhenologyMMS model V1.2 (http://arsagsoftware.ars.usda.gov; McMaster et al., 2005) simulates the sequential phasic development of wheat, barley, maize, sorghum, sunflower, proso millet, and hay millet, according to predetermined thermal time (or number of leaves) for the extremes of either no water deficit or significant (but not lethal) water deficits. For each crop, the developmental sequence of the shoot apex is correlated with developmental stages (e.g., Fig. 10–2 and Fig.10–3 show sorghum). Default parameter values are provided for each crop, but can be changed by the user if desired. The standalone version of this program has no water balance submodel, so it assumes the two extremes of available water mentioned previously. The user could adjust the parameter values to an intermediate value if water deficits are considered between the extremes. The approach used is similar to SHOOTGRO in that water deficit alters the thermal time (as phyllochron or number of leaves) required between a phase according to the empirical responses observed for a crop. Some cultivar options are available for certain crops. Work is ongoing to add more crops, cultivars, and verify estimated phenological responses to water deficits.

Models can be used to test hypotheses when appropriately structured. Four hypotheses that might explain the phenological responses to water deficits were presented. However as previously noted, it is both difficult to experimentally test and distinguish among the individual hypotheses. Existing models do not describe physiological processes in sufficient detail, nor do they have the structure to adequately test Hypotheses 2, 3, and 4. Models such as Sirius and ECOSYS (Grant et al., 1995) that simulate canopy energy balance could be used to test Hypothesis 1 (i.e., that water deficits lead to higher canopy temperatures that alter developmental rates through a thermal response). Unpublished work by Jamieson and Porter (1998) using the Sirius model for the UK examined Hypothesis 1 in studying anthesis dates. They found that higher canopy temperatures under water deficits could account for about 2 d, but this was insufficient to explain fully the observed earliness of anthesis under water deficit conditions. These results match the experimental data presented in Table 10–2 and suggest that increased canopy temperatures can only partly explain phenological responses to water deficits.

A further complication of using these models to test Hypothesis 1 is the difficulty in accurately simulating the genotype responses observed in Table 10–2. Genotypic differences in canopy temperature can be simulated only through factors that affect the energy balance (e.g., canopy size, canopy architecture through the extinction coefficient, and rooting depth that may affect the ability to take up water). There cannot be specific "genotypic" canopy temperature effects, as the physics does not allow it. Therefore, the better question than whether models can be used to test hypotheses might be whether models can accurately do so in a manner that aids in understanding the biology. In this regard, models do not seem to be able to do so.

Improving Phenology Simulation for Water Deficits

To understand better how water deficits influence phenology, the foremost need is better quantification of differences among crops and cultivars to water stress. Ultimately, the goal is a phenology algorithm that accounts for plant developmental differences as a function of temperature, photoperiod, water stress, etc., which describes the genotype by environment interaction for phenology. This algorithm may require modification of existing algorithms or the development of new algorithms. Building on the meta analysis provided in Table 10–1, researchers can create shoot apex developmental sequences and phenology diagrams (e.g., Fig. 1-–2 and Fig. 10–3) that can be used as the basis for simulating phenological responses to varying water stresses.

Once the empirical responses are known for a crop, algorithms for phenology submodels must be created to reflect these responses. Models such as SHOOTGRO and PhenologyMMS already explicitly reflect these responses by modifying thermal time estimates based on varying water levels, but improvements on their thermal time approach now exist and should be incorporated. Work remains to construct still more elegant depictions of development in all crops. For instance, the temperature response curve is assumed to be linear between two threshold levels of water deficits. Additionally, insufficient knowledge exists to incorporate specific adjustments to portray genotype response. If models do not explicitly incorporate phenological responses to varying water deficits, then this enhancement would be in order. In sequential phase models like CSM–Cropsim–CERES Wheat (Hoogenboom et al., 2004; Hunt and Pararajasingham, 1995; Jones et al., 2003; Ritchie, 1991) and AFRCWHEAT2 (Weir et al., 1984; Porter, 1984, 1993), two approaches for simulating the responses could be implemented based on their modified thermal time approach used. One possible modification would be to alter the predetermined thermal development units based on soil water availability; an alternative would be to add a water stress-dependent factor to the modified thermal time approach as implemented in CSM-CROPGRO.

Conclusions

Many models can predict phenology accurately based on the primary driver of temperature, and when appropriate, photoperiod. However, few models have directly addressed phenological responses to water deficits, partly because our knowledge of phenological responses to water deficits is limited. Complicating the simulation of phenological responses to water deficits is the lack of a clear understanding of the mechanisms controlling the developmental responses among crop species and cultivars to varying water deficits that occur at different times in the plant life cycle. As a result, existing algorithms have little mechanistic basis. The goal is to integrate functional genomics with whole plant physiology to understand better plant development as affected by its environment. In turn, this knowledge will foster construction of more robust and accurate crop models.

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